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Boon, P.; Visser, G.H.; Daan, S

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FEEDING AND GROWTH OF JAPANESE QUAIL (*COTURNIX C. JAPONICA*) CHICKS WITH UNPREDICTABLE FOOD ACCESS

by

POLLY BOON^{1,*}, G. HENK VISSER^{1,2} and SERGE DAAN¹

(¹ Zoological Laboratory, University of Groningen, Haren, The Netherlands; ² Centre for Isotope Research (CIO), University of Groningen, Groningen, The Netherlands)

ABSTRACT

We investigated the effect of unpredictable feeding times on feeding activity and body mass gain in fast growing Japanese quail (*Coturnix c. japonica*) from 7 to 31 d of age. Quail chicks were subjected to a long day length (18L:6D) with ad libitum food during (1) 17.5 h of the light period, starting 0.5 h after lights-on (group A, $n = 14$), (2) 6 h of the light period, starting 0.5 h after lights-on (group B, $n = 14$), and (3) 6 h of the light period, starting pseudorandomly either 0.5, 6, or 11.5 h after lights-on (group C, $n = 12$). We examined the effects on locomotor, feeding and drinking activity, body mass, and food intake. Treatment did not affect daily locomotor, feeding, or drinking activity. Distribution of activity over the light period was affected: group B and C showed more activity above the feeder and water container outside the feeding time, and showed a large bout of locomotor and feeding activity at the start of this period. Both overall weight gain and gross energy intake (GEI) were highest in group A and lowest in group C. Distribution of food intake throughout the daily feeding period was affected: group B and C consumed more food during the first part of the feeding period than group A. Daily GEI in group C was influenced by fasting duration prior to feeding and by time of food availability. We suggest that young quail adjust their feeding behaviour in response to their instantaneous energy needs. This effect is modulated by time of food availability: food arriving later in the day led to higher intake levels.

KEY WORDS: *Coturnix c. japonica*, unpredictable feeding, growth, behaviour.

INTRODUCTION

Exposure to food restriction, by either reducing the daily amount of food offered or limiting the time during which feeding can occur, is known to have detrimental effects on body mass gain in juvenile birds (BLANK *et al.*, 1991; BARASH *et al.*, 1992; GEBHARDT-HENRICH & MARKS, 1993; PALO *et al.*, 1995; LEILI *et al.*, 1997). When subjected to such a condition, chicks can adopt different strategies to maximise weight gain.

* Corresponding author; E-mail: P.Boon@rikilt.wag-ur.nl

They may reduce 24-h energy expenditure by decreasing activity during the time no food is present. In this way more energy will be available for body mass increase. When food restriction is imposed by reducing the time during which food is available, birds can also try to improve weight gain by increasing food intake rates. This may be achieved by enlarging (external or internal) hoarding (POWERS, 1991; BARTNESS & CLEIN, 1994; BASCO *et al.*, 1996; WOOD & BARTNESS, 1996). In most experiments where food restriction is imposed via time limitation, food arrives daily at the same time. From these studies it is difficult to understand what controls feeding motivation during food restriction. Experiments that combine food restriction with a fixed daily scheduling of food availability, do not distinguish between a number of possible mechanisms that may control food intake rates: (a) the instantaneous energy deficit as built up by a prior fast, (b) the learnt anticipation of the subsequent fasting interval, and/or (c) the circadian time at which food is expected. To start unravelling some of these potential factors in feeding motivation, we studied the effects of daily predictability of feeding in growing birds. Exposing adult birds to unpredictable feeding regimes has shown that they are able to regulate their internal and external energy reserves in response to recent experience or in anticipation of requirements (DAWSON & MARSH, 1986; JENNI & JENNI-EIERMANN, 1987; BEDNEKOFF & KREBS, 1995). In Great tits (*Parus major*) body mass increase in response to unpredictable feeding conditions was shown to be an adjustment to the feeding circumstances as experienced in the previous few days (BEDNEKOFF & KREBS, 1995). In both mammals and birds it is known that the circadian system plays an important role in the anticipation of feeding schedules (BOULOS *et al.*, 1980; COLEMAN *et al.*, 1982; MISTLBERGER, 1993; PHILLIPS *et al.*, 1993; ONO *et al.*, 1996). When in rats feeding is restricted to a single meal scheduled at a fixed time, the animals show increased locomotor activity before feeding time (BOULOS *et al.*, 1980; HONMA *et al.*, 1987; MISTLBERGER & MARCHANT, 1995; ONO *et al.*, 1996). This prefeeding activity in rats occurs only when food is offered at intervals near 24 h (ASCHOFF, 1986).

In most studies that addressed the effect of unpredictable feeding conditions on food intake and body mass in adult birds, animals were not food restricted: birds were given the choice of either increasing (by enlarging fat reserves) or maintaining their body mass (EKMAN & HAKE, 1990; HURLY, 1992; BEDNEKOFF & KREBS, 1995; GOSLER *et al.*, 1995; WITTER *et al.*, 1995). It is not known how animals respond to unpredictable feeding regimes when subjected to food restriction. We therefore studied the effect of unpredictable and restricted feeding conditions on body mass and feeding behaviour in growing Japanese quail (*Coturnix c. japonica*). Japanese quail has the fastest growth rate in the family Phasianidae

(RICKLEFS, 1973), and is likely to be responsive to variations in food availability. In growing animals a substantial amount of the energy intake is needed for growth. It is plausible that unpredictable, restricted feeding conditions during early development may be more critical than in adults with serious consequences for both future reproduction and survival. We subjected the chicks to either of three different feeding regimes: 17.5 h feeding, 6 h feeding with the start of the feeding period at a fixed time every day, and 6 h feeding with the start of the feeding period at an unpredictable time every day. These schedules were chosen to separate the effects of food restriction from those of the predictability of a restricted schedule. We examined the effects on locomotor, feeding and drinking activity, body mass, food intake, and 24-h distribution of food intake throughout juvenile development.

MATERIAL AND METHODS

Animals, experimental set up, and housing

Japanese quail (*Coturnix c. japonica*) neonates, of a strain selected for maximum body mass at the age of 5 weeks, were obtained from a commercial quail farm (N.V. Nouwen, Lommel, Belgium). Until the age of 6 d the birds were kept in wooden cages ($l \times b \times h$: $67 \times 39 \times 44$ cm³) with sawdust bedding in continuous light and ad libitum access to quail starter food and water, to ensure maximum possible body mass gain. A 40 W heating lamp was placed in each cage to provide a temperature gradient sufficient for selection of the preferred temperature by the chicks. At 6 d of age the birds were assigned to the experimental conditions in such a way that the average body mass did not differ between the groups. A long day length (18L:6D) was used for all groups throughout the experiment. Group A ($n = 14$) was allowed to eat during 17.5 h of the light period, starting 30 min after lights-on. Group B ($n = 14$) had ad libitum food during 6 h of the light period, starting 30 min after lights-on every day. Group C ($n = 12$) had also ad libitum food during 6 h of the light period, but food was offered at three different times on different days: (1) 30 min after lights-on (comparable to group B; Early), 6 h after lights-on (Middle), or (3) 11.5 h after lights-on (Late). In this way the link between food availability and lights-on was broken. The sequence of the three times was pseudorandomly chosen, so that E, M, and L occurred with equal frequency in the experiment, which lasted 24 d (E, M, L, M, L, E, M, L, E, E, M, L, L, E, L, E, M, M, E, L, M, L, M, E). At 6 d of age, the animals were permitted to habituate to the experimental conditions and allowed to eat ad libitum during the whole 24-h period. The experiment

started at the age of 7 d. Throughout the experimental period a pellet-diet (Institute for Animal Science and Health, ID-DLO, The Netherlands) containing 27.7% (w/w) crude protein and 17 kJ-wet g⁻¹ (gross energy content as determined by bomb calorimetry; own measurement) was used. Water was freely available.

During the experiment the animals were housed in wooden cages ($l \times b \times h$: $67 \times 39 \times 44$ cm³) with a wire bottom and a 40 W heating lamp. The heating lamp was gradually raised and finally removed to allow the ambient temperature to decrease to room temperature ($\sim 21^\circ\text{C}$) within 3 weeks of age. The birds were housed in pairs except for four cages in group B and two cages in group C with only one bird. This was due to mortality and aggression between birds, and did not affect overall weight gain. One feeder and one water container were mounted on the left and right side of the cages, respectively, and separated from the inside of the cage by a partition containing two openings, one for each bird. Feeders were automatically removed and returned using a clock-controlled compressed air system.

Activity, body mass, and food intake

Locomotor activity was continuously recorded by passive infrared detectors (PID, Wonderex FX-35) placed in the centre above six cages of both group A and B, and eight cages of group C. Feeding and drinking attempts were recorded as interruptions of an infrared beam (XUL-M06031, Telemécanique, France) located above the feeder and the water container. Feeding activity was recorded in three, seven, and six cages of groups A, B, and C, respectively. The number of cages for drinking activity were three, five, and six, respectively. All movements were automatically recorded on a computer every 2 min throughout the experiment and expressed as the number of movements per bird.

Birds were weighed (to 0.1 g) daily before food became available, and every hour afterwards over 6 h to obtain a measure for the distribution of food intake over the feeding period. We are aware that by this procedure birds of the different groups were not proportionally disturbed (group B and C every hour of the feeding period and group A at only one third of that period), which may have affected daily food intake, and consequently body mass. Since weighing took less than a minute per animal, this effect is probably negligible compared to the treatment effect. We chose for weighing the birds hourly instead of the feeders because of food spillage: the time needed to collect spilled food would have interfered with the restricted feeding time. Total daily food intake (g) was measured by weighing the feeders every morning just after lights-on. Spilled food was carefully collected from all parts of the cage and at the side of

the cage where the feeder was located. Daily gross energy intake (GEI) was calculated by transforming daily food intake (g) into its energetic equivalent ($17 \text{ kJ} \cdot \text{g}^{-1}$). This value was expressed as GEI per bird. To obtain the daily "growth efficiency" ($\% \cdot \text{d}^{-1}$), the change in body mass per 24 h was divided by the amount of food (g) eaten over the same period.

Data analysis

Data are expressed as means and inter-individual standard deviations. Differences between group means were analysed posthoc by Tukey's "honestly significant difference" test, after an effect of treatment on the variable of interest was ascertained by ONEWAY analysis (SPSS Inc., 1988). Student's *t* test was used when comparing only two groups. Analysis of covariance (ANCOVA) was applied, after logarithmic transformation of gross energy intake and body mass, to test for the effect of treatment and treatment \times body mass interaction on gross energy intake after correction for body mass. ANCOVA was also used to test for the effect of hours fasting prior to feeding and time of food arrival, and possible interaction terms, on gross energy intake in group C, after correction for body mass. This ANCOVA procedure is an *a posteriori* test without preplanned comparisons and the statistics should be evaluated conservatively (NORUŠIS, 1988). Therefore, interaction terms were removed when $p \geq 0.02$. The repeated measures procedure was applied to test for the effect of treatment on the distribution of food intake over the first 6 h of the feeding period. Tests were two-tailed, and significance was accepted at $p < 0.05$.

RESULTS

Locomotor, feeding, and drinking activity

In figure 1 we plotted representative daily locomotor, feeding and drinking activity patterns for the three groups. Points depict the average activity over all cages during a 24-h period. For group C activity levels were plotted for the three different times of food arrival after an 18-h fast. We chose for an 18-h fast, because of its comparability with the daily fasting duration of group B. Locomotor activity pattern of all groups was highly synchronised with the light-dark cycle (fig. 1). In all groups more than 90% of the locomotor activity over the whole experiment occurred during the light episode: $91.4 \pm 1.8\%$ in group A, $96.9 \pm 0.7\%$ in group B, and $96.5 \pm 1.0\%$ in group C. About one third of the locomotor activity during the light episode in group B and C occurred during feeding time

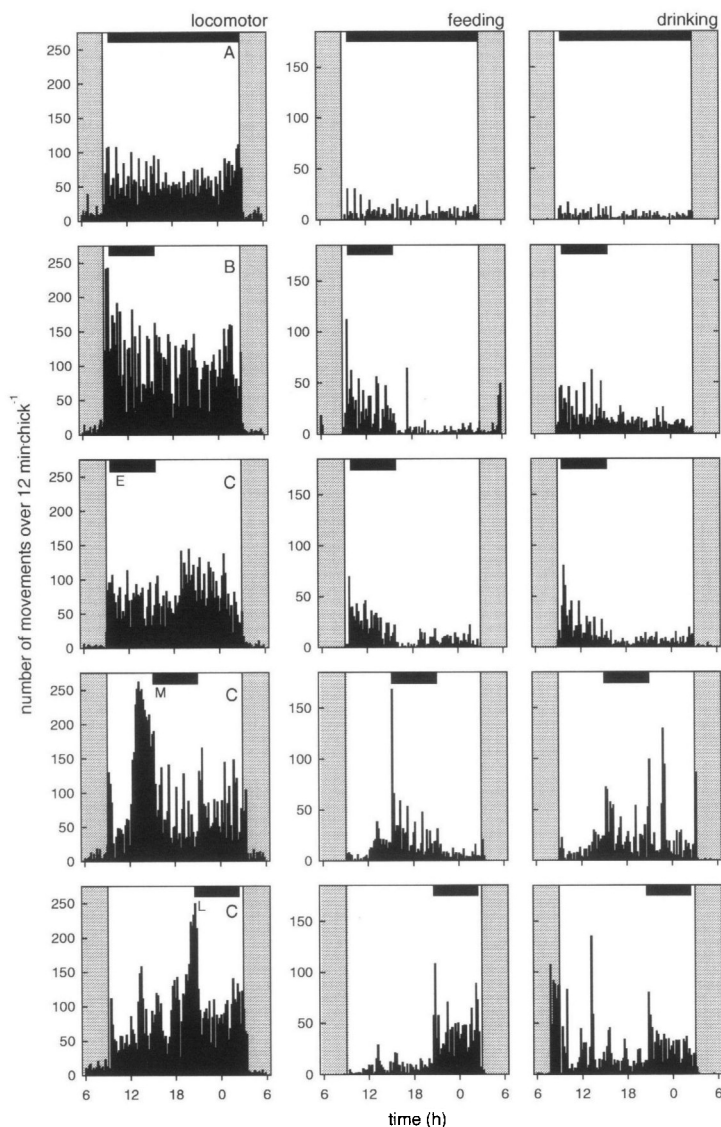


Fig. 1. Representative plots of daily locomotor, feeding and drinking activity of Japanese quail chicks subjected to 18L : 6D with food available during (1) 17.5 h of the light period, starting 30 min after lights-on (group A), (2) 6 h of the light period, starting 30 min after lights-on (group B), and (3) 6 h of the light period, starting either 0.5 (E), 6 (M), or 11.5 h after lights-on (L; group C).

(equivalent to the duration of the feeding period compared to the light period): $31.4 \pm 2.7\%$ and $26.3 \pm 5.4\%$, respectively. The average 24-h locomotor activity, calculated over the total experimental period, was not affected by treatment: 5793 ± 586 movements \cdot d $^{-1}$ for group A, 6441 ± 1887 movements \cdot d $^{-1}$ for group B, and 7917 ± 2070 movements \cdot d $^{-1}$ for group C. The distribution of activity was influenced by treatment (fig. 1). In group C the postponement of the feeding period to later hours was associated with an irregular locomotor activity pattern, which became more stable at a lower level after food arrival (fig. 1). There was a rise in locomotor activity in anticipation of food arrival that was absent in group A, and group C on days with early (E) feeding (fig. 1).

In group A $99.8 \pm 0.1\%$ of all activity above the feeder and the water container over the total experimental period occurred during the time of food availability (fig. 1). In group B and C activity above the feeder was highly correlated with the presence of food, with a peak in activity at the start of food access. In group C this peak showed a tendency to increase when food arrival was postponed to later hours in the day (fig. 1). After this initial peak, activity above the feeder subsided during the subsequent hours of food access, except in group C at time L: activity remained relatively high and increased at the end of the feeding period (= start of the night). Calculated over the total experimental period $71.5 \pm 10.9\%$ of all activity above the feeder in group B and $63.0 \pm 12.5\%$ in group C occurred during the period of food availability (fig. 1). Drinking was less restricted to this period (fig. 1): in group B $58.8 \pm 5.2\%$ of all activity above the water container occurred during food availability, and in group C $45.8 \pm 8.7\%$. Activity above the water container was especially high in group C when food arrived later in the day (fig. 1). The number of movements above the feeder per 24 h over the total experimental period was not influenced by treatment: 922 ± 280 movements \cdot d $^{-1}$ for group A, 1374 ± 815 movements \cdot d $^{-1}$ for group B, and 1395 ± 329 movements \cdot d $^{-1}$ for group C. This was also true for the total number of movements above the water container per 24 h: 686 ± 39 movements \cdot d $^{-1}$, 1473 ± 2617 movements \cdot d $^{-1}$, and 1701 ± 752 movements \cdot d $^{-1}$, respectively.

Weight gain

Figure 2A compares body mass (g) development against age (d) for the experimental groups. At 7 d of age, when food restriction was introduced, group B and C did not gain weight during the first 2 d. After that weight increased again, but the birds did not reach the same body mass as birds of group A at the end of the experiment. The total body mass increase was highest in group A (194 ± 24 g), and lowest in group C (99 ± 23 g). Group B was intermediate (133 ± 25 g; $F_{2,39} = 54$, $p < 0.0001$).

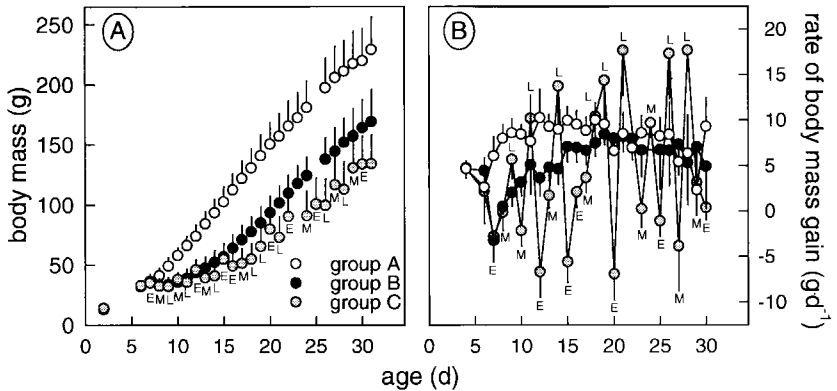


Fig. 2. (A) Mean body mass (g) and (B) mean rate of body mass gain ($\text{g}\cdot\text{d}^{-1}$) as a function of age (d) in three groups of Japanese quail: group A (open symbols), B (closed symbols), and C (grey symbols). E, L and M indicate feeding times in group C. Vertical lines indicate SDs. For more details see figure 1.

The rate of body mass gain ($\text{g}\cdot\text{d}^{-1}$) varied with experimental period (fig. 2B). Group A showed the highest rate of weight gain during the first 12 d of the experiment. Group B had a low rate of weight gain during the initial part of the experiment, but increased its weight gain rate to the level of group A at 19 d of age. In group C weight gain rate fluctuated: days of rapid weight gain alternated with days of low or no increase in body mass.

Gross energy intake

Mean daily gross energy intake (GEI; $\text{kJ}\cdot\text{d}^{-1}$) of quail for all treatments is plotted as a function of age in figure 3. Mean daily GEI over the total experimental period was highest in group A ($324 \pm 32 \text{ kJ}\cdot\text{d}^{-1}$), and lowest in group C ($171 \pm 30 \text{ kJ}\cdot\text{d}^{-1}$). Group B was intermediate ($213 \pm 19 \text{ kJ}\cdot\text{d}^{-1}$; $F_{2,22} = 61$, $p < 0.0001$). It is evident from these figures that the decrease in GEI in group B and C was not proportional to the reduction in feeding time. After incorporating mean body mass as a covariate in ANCOVA, the effect of treatment on GEI remained significant ($F_{2,19} = 35$, $p < 0.001$). Treatment \times body mass interaction did not significantly contribute to the explained variance.

The difference in mean daily GEI between group B and C, despite equal daily food availability, was due to the variability in both fasting duration prior to feeding and time of food arrival (fig. 1) in group C. The best way to analyse the effect of these two factors on GEI would be to include both simultaneously in a single ANCOVA, and test the

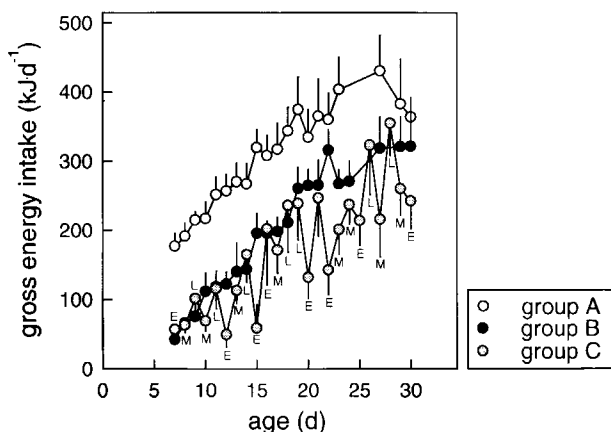


Fig. 3. Mean daily gross energy intake ($\text{kJ}\cdot\text{d}^{-1}$) in relation to age (d) in three groups of Japanese quail: group A (open symbols), B (closed symbols), and C (grey symbols). E, L and M indicate feeding times in group C. Vertical lines indicate SDs. For more details see figure 1.

contribution of each to the explained variance. However, by manipulating the sequence of feeding time we could not control simultaneously for fasting duration. Length of fasting was therefore not evenly distributed over the three feeding times, making an analysis with repeated measures not feasible. We therefore analysed the effect of fasting duration on mean GEI corrected for body mass ($\text{kJ}\cdot\text{d}^{-1}\cdot\text{g}^{-1}$) within group C irrespective of feeding time. ANCOVA revealed that mean GEI varied significantly with fasting duration ($F_{4,35} = 86$, $p < 0.0001$; fig. 4). Up to an 18-h fast, an increase in fasting duration was related to an increase in GEI. Fasting for more than 18 h did not increase GEI any further. Daily GEI per g animal ($\text{kJ}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$) after an 18-h fast was significantly higher in group C than group B, $3.4 \pm 0.3 \text{ kJ}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$ and $2.6 \pm 0.2 \text{ kJ}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$, respectively ($T_{14} = -5.8$, $p < 0.001$). To examine the effect of feeding time on mean GEI, we calculated the mean daily GEI per g animal ($\text{kJ}\cdot\text{d}^{-1}\cdot\text{g}^{-1}$) for the three feeding times, irrespective of fasting duration. Time of food arrival significantly influenced daily GEI ($F_{2,21} = 158$, $p < 0.0001$): GEI was lowest at time E ($1.9 \pm 0.2 \text{ kJ}\cdot\text{d}^{-1}\cdot\text{g}^{-1}$), intermediate at time M ($2.4 \pm 0.1 \text{ kJ}\cdot\text{d}^{-1}\cdot\text{g}^{-1}$), and highest at time L ($3.5 \pm 0.2 \text{ kJ}\cdot\text{d}^{-1}\cdot\text{g}^{-1}$).

The mean daily growth efficiency ($\%\cdot\text{d}^{-1}$) was stable throughout the study in group A (fig. 5). The two restricted groups had a negative growth efficiency at the start of the experiment. In group B growth efficiency increased rapidly and reached the same level as in group A after 5 d. The growth efficiency in group C showed an irregular pattern: days with a high efficiency alternated with days of low or negative efficiency. Overall

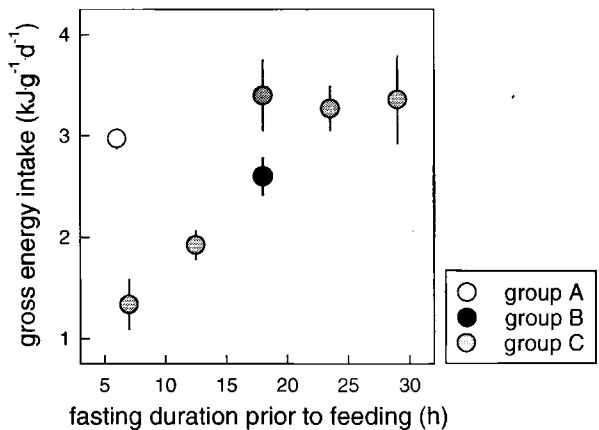


Fig. 4. Relationship between daily gross energy intake, after correction for body mass ($\text{kJ}\cdot\text{g}^{-1}\cdot\text{d}^{-1}$), and amount of hours fasting prior to feeding (h) in three groups of Japanese quail: group A (open symbols), B (closed symbols), and C (grey symbols). Values are means, and vertical lines indicate SDs. For more details see figure 1.

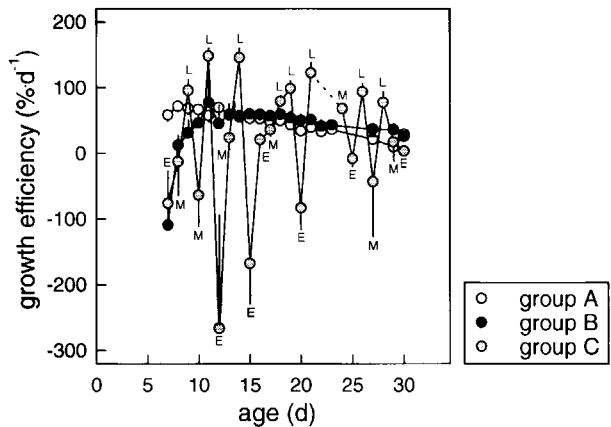


Fig. 5. Mean growth efficiency ($\%\cdot\text{d}^{-1}$) as a function of age (d) in three groups of Japanese quail: group A (open symbols), B (closed symbols), and C (grey symbols). E, M and L indicate feeding times in group C. Vertical lines indicate SDs. For more details see figure 1.

growth efficiency (total food intake over the whole experimental period per cage/total body mass increase over the same period per cage; %) varied significantly with treatment ($F_{2,22} = 22$, $p < 0.0001$). Overall growth efficiency was highest in group A ($49 \pm 2\%$), and did not differ significantly between group B ($44 \pm 2\%$) and C ($42 \pm 3\%$).

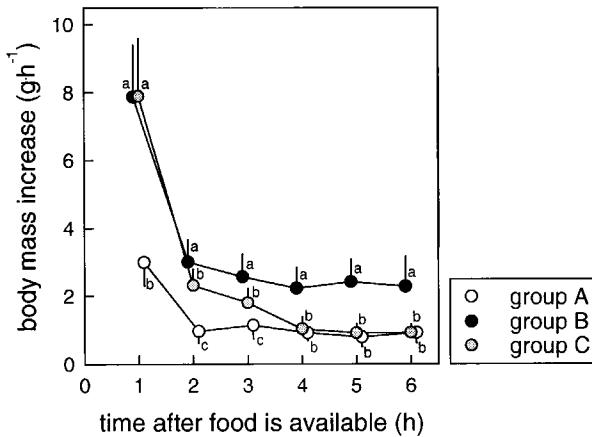


Fig. 6. Distribution of food intake, calculated as weight increase per h ($\text{g}\cdot\text{h}^{-1}$), during the first 6 h of the feeding period in three groups of Japanese quail: group A (open symbols), B (closed symbols), and C (grey symbols). Values are means, and vertical lines indicate SDs. Means with the same letter within 'time after food is available' differ not significantly ($p > 0.05$) from each other (Tukey's "honestly significant" test). For more details see figure 1.

In figure 6 we plotted the distribution of food intake, calculated as body mass increase per hour, for the first 6 h of food availability, regardless of fasting duration and time of food access in group C. Distribution of food intake varied significantly with treatment ($F_{2,37} = 129$, $p < 0.001$). Group B and C consumed significantly more food during the first 3 h of feeding than group A. During the last 3 h of food availability, group B had a higher intake than both other groups. No increase in food intake was visible at the end of the feeding period in group B and C.

DISCUSSION

This experiment showed that growing quail exposed to unpredictable feeding conditions gain less body mass than birds that receive the same amount of food per day but at fixed times. Quail chicks appear to respond mainly to these unpredictable conditions by adjusting their food intake in response to their energy needs as experienced at the time of feeding, which is mainly determined by the length of the fasting period prior to feeding. Time of food availability also seemed to influence feeding motivation in chicks: food arriving later in the day induced higher intake levels.

Growing quail subjected to unpredictable feeding circumstances had a lower body mass than birds offered the same amount of food per day but at fixed times (fig. 2A). If chicks could anticipate fasting periods of unpredictable length or respond to the feeding conditions as experienced in the previous days, food intake should be consistently high and only depend on the size of the animal. In growing quail subjected to an unpredictable feeding regime food intake was highly variable: days of high intake alternated with days of low intake (fig. 3A). This fluctuation in food intake was determined by the variation in fasting duration prior to feeding (fig. 4), indicating that the birds respond to their instantaneous energy needs. We also showed that the birds of group C had a higher gross energy intake (GEI) when they had fasted for 18 h than birds that fasted for 18 h every day (fig. 4). This could signify that the birds of group C do adjust to some extent to experience and consume more food than when they are subjected to the same fasting duration every day. Alternatively, these chicks, after an 18-h fast, have larger energy deficits, because of their irregular feeding pattern during the previous days. Another determinant of feeding motivation was the time at which food became available: chicks of group C, after an 18-h fast, had higher feeding activity levels at time L (fig. 1), and GEI seemed to increase when food arrived later in the day. Time of day is a well-established regulator of food intake and weight gain in a number of species. In free living birds eating is sometimes shifted to the end of the day. This may minimise the risk of predation (heavy birds are more vulnerable through decreased agility) or reduce the cost of flight (DAAN & ASCHOFF, 1982; LIMA, 1986; MCNAMARA & HOUSTON, 1990; MCNAMARA *et al.*, 1994). This applies to flying birds. The young quail investigated here are flightless, and furthermore highly domesticated, making a relation of feeding behaviour with predation risk doubtful. More likely, spending part of the light period in anticipation of food arrival augmented feeding motivation. Although our design does not permit to distinguish between the effect of fasting duration and time of food arrival on feeding motivation, the results suggest that both factors contribute to overall feeding motivation.

In poultry restrictive feeding results in higher levels of locomotor and/or drinking activity compared to ad libitum conditions (HOCKING *et al.*, 1993; SAVORY & MAROS, 1993). In our study we did not find an effect of treatment on either total locomotor, feeding or drinking activity. All three types of activity showed merely a tendency to higher levels in group B and C. Locomotor activity in group C had a more irregular pattern when food arrival was delayed to later hours in the day compared to early in the day, and compared to the activity pattern of both groups with fixed feeding times (fig. 1). This indicates that the chicks become restless during

food unavailability, possibly searching for food. The daily distribution of movements above the feeder and the water container was affected by treatment. In group A more than 99% of all activity above the feeder occurred during the time of food availability, while in group B and C this percentage was 60-70%. Group C showed a large increase in feeding (and locomotor) activity at the start of food access that increased dramatically when food arrival was delayed to later hours in the day. Also group B showed an increase in both activity levels at the start of food availability, but less pronounced than in group C at time M and L (fig. 1). These activity bouts far exceeded the initial activity bouts in group A (fig. 1), and support the large bout in food intake during the first feeding hours in group B and C (fig. 6). These birds apparently had learned to eat as much as they could as soon as food became available. Birds in group C also showed an increase in activity above the feeder at the end of the feeding period when food arrived late in the day (time L). Broilers have been shown to be able to anticipate periods of food unavailability when this coincided with darkness: they consume more food at the end than at the onset of the feeding period (MAY & LOTT, 1992). These birds were unable to anticipate a fasting period when exposed to continuous light: more food was consumed at the onset of the feeding period. Similarly, rats have a feeding peak at the end of darkness (= feeding period), which is advanced by advancing the light by 2 h, but not by advancing the onset of fasting by 2 h (KERSTEN *et al.*, 1980). In group B and C the end of food availability only coincided with darkness when food arrived late in group C, which may explain why under the other conditions chicks did not show an increase in food intake at the end of the feeding period. In group B and C a large part of the drinking activity (in group C even more than 50%) occurred outside the feeding period, while under ad libitum conditions drinking coincided mainly with feeding. This may be another indicator that the chicks are restless, possibly exploring their water containers in search of food. Because the total activity was not different between group B and C, a difference in energy expenditure is not likely to be an explanation for the difference in weight gain between these two groups.

GEI in both group B and C was reduced compared to group A, although the reduction was not proportional to the decrease in feeding time. The chicks in these groups learned quickly that food was present during a part of the day only. Already on the second day of the experiment the birds started to exploit their crop for temporary food storage that was mobilised when no food was available. In this way chicks could consume more food than expected on the basis of time reduction only. This strategy allowed group B to gain weight continuously after an initial drop during the first 2 d of the experiment (fig. 2A). They increased both weight gain rate

(fig. 2B) and growth efficiency (fig. 5) to the level of group A. Group C followed the same strategy, but with a different result for weight gain and GEI. Fasting duration in this group was not constant: days of only 7 h fasting alternated with days when the duration of fasting could be as long as 29 h. After fasting for only 7 h, the crop (and digestive tract) may still be largely filled with food. This would explain the low feeding motivation of these birds when feeding time E was preceded by feeding time L (fig. 3). Consequently food intake was too low to cover the energy needs of the birds during the following fasting period and they lost weight. When the birds had been fasting for 18 h or more the crop (and digestive tract) may have been empty and feeding motivation was high (fig. 4). In quail the control of feeding is concerned with emptying and filling of the digestive tract including the crop rather than with changing levels of circulating nutrients (SAVORY, 1980). The irregular distribution of food intake in group C resulted in large fluctuations of weight gain (days of low or no weight increase alternated with days of high weight increase) and a lower overall GEI as compared to group B. It is likely that both this difference in food consumed and the irregular distribution of intake resulted in a difference in overall weight gain between group B and C. In hamsters unpredictable food deprivation has a more suppressive effect on weight gain than shortage of food as such (IBUKA *et al.*, 1993). Time of daily food arrival most likely modulated the effect of crop (and digestive tract) contents on feeding motivation (fig. 1).

Periodic daily food availability activates several processes in the body in anticipation of food arrival (COMPERATORE & STEPHAN, 1987; SCHWARTZ *et al.*, 1990; KWAKKEL *et al.*, 1993). In rats the gastrointestinal tract anticipates the time of feeding by increasing duodenal activity and levels of digestive enzymes 2-4 h prior to food availability (COMPERATORE & STEPHAN, 1987). In this way a high efficiency of food digestion is accomplished. When food is offered at unpredictable times, the animal may not be able to synchronise feeding with anticipatory digestive processes, and digestion may be less efficient than in animals subjected to predictable feeding times. This may also partly explain the difference in weight gain between group B and C. Uncertain situations, even when unrelated to food restriction, can have a detrimental effect on body mass (MCGRADY & CHAKRABORTY, 1983; IBUKA *et al.*, 1993; MEERLO *et al.*, 1996). It seems plausible that also our birds experienced the unpredictable feeding conditions as more trying, with a more suppressive effect on body mass.

In conclusion, the study showed that growing quail, subjected to either predictable or unpredictable restricted feeding conditions, quickly learn that feeding is only possible during a limited number of hours per day. To

cope with these circumstances, the birds exploit their crop (and digestive tract) as a temporary storage place for food that is mobilised during the time that feeding is not possible. Restricted birds with fixed feeding times (group B) were thereby able to resume the same weight gain curve as group A with a delay of about 5 d (fig. 2A). Restricted birds with unpredictable feeding times (group C) seemed to adjust their feeding strategy to the fasting duration prior to feeding. The young birds respond to their energy needs of the moment and seem neither to anticipate fasting periods, nor to respond to feeding conditions as experienced on previous days. They thereby showed a further retardation in body mass compared to quail chicks on a daily constant restricted feeding regime. This response to energy needs was modulated by time of food arrival: motivation was higher when feeding time was delayed to later hours in the day. Predictable daily variations in food supply offer the opportunity for better adaptive adjustments of food intake and weight gain than unpredictable variations.

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